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The subspecific status of European populations of the striped field mouse *Apodemus agrarius* (Pallas, 1771) based on morphological and biochemical characters

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Abstract. Patterns of geographic variation in 13 populations of *Apodemus agrarius* from Kaliningrad (GUS) to Macedonia were investigated by means of skull morphology (14 variables) and in a subset of 4 populations by electrophoresis (44 enzymes encoded by 57 gene loci). Genetic distance analysis of biochemical data failed to indicate clusters of populations differentiated at the subspecific level. Morphological differences were mainly size-dependent. Linear skull dimensions could be attributed to non-genetic, environmental adaptations with the exclusion of molars which seem to be relatively invariable against environmental conditions. Selective constraints to modify parts of the dentition seem to require stronger changes in the genetic program that may vary between different populations to a low degree. Looking at all results, *A. a. kahmanni* shows convergent size relationships to *A. a. istrianus*. *A. a. kahmanni* is in geographic contact with populations of the nominal race, and its larger cranial proportions are possibly a result of clinal size variation. By contrast, *A. a. istrianus* is geographically isolated and appears to establish specific genetical characteristics as expressed by a highly significantly reduced heterozygosity and morphological features similar to those of *A. a. kahmanni*.

Key words. Mammalia, Rodentia, *Apodemus agrarius*, subspecies, geographic variation, Europe, craniometry, Multiple Group Principal Component Analysis, electrophoresis, genetic distances.

Introduction

The striped field mouse (*Apodemus agrarius*) inhabits a wide geographical range between central Europe in the west and China and Korea in the east (Musser & Carleton 1993). In Middle Europe three subspecies of *Apodemus agrarius* have been discussed: *A. a. henrici* von Lehmann, 1970 from Germany, regarded by some authors (e.g. Böhme 1978) as a synonym of *A. a. agrarius*, *A. a. istrianus* Krystufek, 1985 from Slovenia, and *A. a. kahmanni* Malec & Storch, 1963 from Macedonia. While *A. a. kahmanni* is regarded as valid by most authors (Böhme 1978, Kahmann & Einlechner 1992), the status of *A. a. istrianus* was recently questioned by Kahmann & Einlechner (1992).

A. a. henrici was described from Germany (v. Lehmann 1970). Although we had no material from the type locality of *A. a. agrarius* in Russia, we follow Böhme (1978) in synonymizing *henrici* with *agrarius*. *A. a. istrianus* occurs in Slovenia and NE Italy (Krystufek 1985, 1991, for Italy see Sala 1974 and Zulian 1987). According to Krystufek (1985, 1991, pers. comm. 1995) its populations are geographically separated by a gap from east Slovenian populations which represent *A. a. agrarius*. Kahmann (1961) reported on findings from Ribnica, a place right between the two current areas, but he left no voucher specimens and Krystufek (1985) could not confirm this locality after intense collecting. Other authors, however, suggested that all

A. agrarius from the area of former Yugoslavia and NE Italy should be referred to subspecies *kahmanni* (Djulic & Vidinic 1964, Ondrias 1966, Soldatovic et al. 1971, Kahmann & Einlechner 1992).

Descriptions of subspecific divergence among populations of the striped field mouse in Europe were to a great extent based on external morphological traits, mainly differences in size. In this paper, we compare patterns of morphological differentiation among populations assignable to the 3 subspecies currently recognized to their patterns of biochemical differentiation, in order to account for genetic relationships that define evolutionary units such as subspecies. Inasmuch, we follow the concept of Smith & Patton (1988) to consider those entities to have both character (morphological and genetical) and geographic continuity as appropriate infraspecific units to be recognized in a formal taxonomy. While from the Oriental range of the species only little karyotypic (Bulatova et al. 1991) and biochemical data are available (Wang 1985, Zhao & Lu 1986, Liu et al. 1991), the scarce data on European populations are widely scattered in the literature (Britton-Davidian et al. 1991; Filipucci 1992; Gemmeke 1980; Gill et al. 1987; Hartl et al. 1992; Niethammer unpubl.). But, dealing with small sample sizes, they seem not to be sufficient to fully characterize infraspecific genetic variability of *A. agrarius*. The purpose of this study was to assess the taxonomic status of European populations of *A. agrarius* at the border of its range in western Europe. The present multivariate examination of skull proportions in combination with a rigorous analysis of protein variation should give answers whether certain population groups warrant recognition as subspecies or not.

Materials and methods

Morphometry

Measurements: In the craniometric part of the study we examined a total of 158 skulls stemming from 13 populations between Kaliningrad (GUS) in the north and Lake Dojran (Macedonia) in the south (Fig. 1). Only young adult and adult specimens of both sexes (tooth-wear classes 3—5 according to Adamczewska-Andrzejewska 1973) were measured in order to reduce variance bias in size and shape introduced into the samples by ontogenetically caused variation. The sexes were not separated (populations sampled and abbreviation codes are given in the legend to Fig. 1).

Skulls are stored in the following collections: Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK); Senckenberg Museum, Frankfurt/M. (SMF); Slovene Museum of Natural History, Ljubljana (PMS); Staatliches Museum für Naturkunde, Görlitz (MNG); private collection H.-J. Pelz, Münster (CP); private collection H. Meinig, Werther/Westf. (CHM).

14 measurements were taken, measurements 1 to 9 (Fig. 2) with a digital calliper (Mitutoyo digimatic) to the nearest 0.01 mm, measurements 10 to 14 with a binocular (Zeiss GSZ) with an enlargement of 50. All measurements were taken by one of us (H.M.). Abbreviations used are: Cbl — condylobasal length (1), zBr — zygomatic breadth (2), IoC — interorbital constriction (3), RoM — rostral breadth (4), NL — nasalia length (5), MBr — mastoid breadth (6), APF — length of anterior palatine foramen (7), MxT — maxillary tooth-row length (8), D — diastema (9), M1L — length of first upper molar (10), M1Br — breadth of first upper molar (11), M2Br — breadth of second upper molar (12), M3Br — breadth of third upper molar (13), ID — incisive diameter (14).

Statistical analyses

Population genetic measures: Allelic frequencies were computed for each population derived from individual electrophoretic genotypes by gene-counting as implemented in the BIOSYS-1

Fig. 1: Geographical origin of the populations examined: 1 — Zehlau, Kaliningrad area (KAL), GUS (7); 2 — Prenzlau, Brandenburg (PRE), Germany (12); 3 — Berlin (ber), Germany (13); 4 — Harz, Lower Saxony (har), Germany (15); 5 — Görlitz, Saxony (goer), Germany (18), 6 — Osthessen (ohe), Germany (16); 7 — Tiszacsege, Hortobagy (tis), Hungary (7); 8 — Radenci, Mura rijeka (rad), Slovenia (21); 9 — Brezice (BRZ), Slovenia (6); 10 — Ajdovscina (AJD), Slovenia (11); 11 — Rovinj (rov), Croatia (15); 12 — Banja Bansko (bba), Macedonia (3); 13 — Lake Dojran (doj), Macedonia (13). Codes for populations studied morphologically and biochemically are given in capitals, codes for populations studied only morphologically are given in lower letters; the numbers of skulls measured are given in parentheses.

program of Swofford & Selander (1981); allele frequency estimates for an isofemale F1 line sample from Kaliningrad area (KAL) were corrected for introduced bias not exclusively screening for polymorphism in samples from the wild (Long 1993). The amount of genetic divergence between populations was computed by Nei's unbiased standard genetic distance D (Nei 1978). A phenogram of the genetic relationships among populations was obtained performing the unweighted pair group arithmetic average cluster analysis (UPGMA, Sneath & Sokal 1973). Standard errors on each bifurcating node were calculated as the standard deviation of all pairwise distances between all OTUs joining the nodes within the cluster consecutively (Nei et al. 1985).

Cranial morphometric analyses: Morphological relationships among geographic samples were assessed by four substantial techniques utilizing several statistical routines of the SYSTAT version 5.03 for DOS (Wilkinson 1990), the BMDP-PC90 package (Dixon 1990) and the NTSYS-pc ver. 1.60 (Rohlf 1990) for IBM-compatible computers.

Techniques for verification of natural groupings (in this case subspecies) should have the property not to be biased by information of group membership, that is an a priori assignment of specimens to these groups (Humphries 1984). As an exploratory technique for discovering structure in data the Principal Component Analysis (PCA) is widely used in systematic studies. Here we employ Multiple Group Principal Component Analysis (MGPCA; Thorpe 1983, 1988). It provides a multivariate means to assess the within-group components of character variation when using intercorrelated linear measurements. By pooling the within-group variance-covariance matrices derived from log-transformed cranial variables it contributes better to among-group discrimination than ordinary PCA. The logarithmic transformation makes the covariance matrix independent of scaling of measurements but standardizes variances and preserves allometries (Jolicoeur 1963). Extracted principal components are interpreted as patterns of covariation in size and shape, but actually do not confuse the within- and between group differences when several groups are used (Thorpe 1976). The first MGPCA axis derived from the pooled within-group variance-covariance matrix can be interpreted as a general within-group allometric "size" vector if most of the original variables contribute with positive signs and equal magnitude to its eigenvector coefficients (Patton & Smith 1990).

The first step of the procedure was the computation of character residuals from the log-transformed variables for each population sample derived from an analysis of variance using the MGLH routine of SYSTAT. An ordinary PCA on the covariance matrix of these residuals produced eigenvectors to be cross-validated by multiplying the score coefficients with the log-transformed variables (using SYSTAT's weighting variable option). Alternatively, computation could be done using BMDP-PC90 tools. First the variance-covariance matrix was computed for each of the 13 groups (= populations), and these were pooled to produce a single within-group variance-covariance matrix using BMDPAM-module. Then from this matrix the principal components were extracted by means of the BMDP4M-routine.

The resulting component scores were used in bivariate plots in an attempt to separate the groups (= populations or subspecies) either "size" included or excluded (omitting MGPC-1 = "size-out" analysis).

Following these latter consideration of a "size-out" analysis (Thorpe et al. 1982), the "size-dependent" principal components (MGPC-1 and also MGPC-2) were excluded from subsequent analyses and the component scores of the MGPCA2-14 res. MGPCA3-14 variates are regarded as size-independent 'characters', which were subjected as new variables to a discriminant analysis to assess grossly size-free variation between populations. Individual scores on the first two canonical axes plotted against each other show size-independent shape variation among the populations.

In a slightly different approach used as an independent means to subsume for effects of overall size on variation found among populations, cranial variables were first size-adjusted, using Burnaby's (1966) canonical variate analysis framework. Data were projected onto the hyperplane orthogonal spaced to the "size"-loaded vector of the first principal component employing the ORTH option of the PROJ module of NTSYS. Individual scores on the adjusted principal components plotted against each other show size-independent discrimination of the populations.

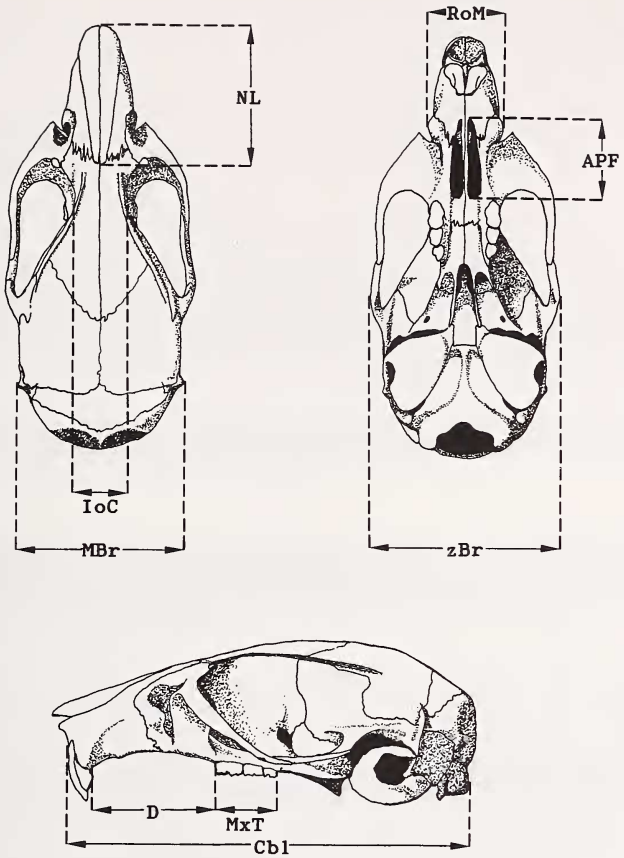

Fig. 2: Skull of *Apodemus agrarius* with the cranial measurements 1 to 9 indicated (measurements 10 to 14 not shown). For abbreviations see text.

Linear Discriminant Function Analysis using the pooled variance-covariance matrix was performed to compute the distances between different samples maximizing the between-group versus the within-group variance. It requires a beforehand allocation of individual specimens to one of the a priori determined groups (Neff & Smith 1979). We graphically demonstrate the differences between the groups (= populations) by a Neighbour-Joining tree (cf. Nei 1987) clustering the Mahalanobis distances of individual canonical variable scores from group centroids. Finding classification functions was computationally realized with the 'Stepwise Discrimination Analysis BMDP-subroutine 7M'. Clustering was done with NTSYS.

Size and shape covary, and unless isometry pertains, such covariation implies a changing relationship between size and shape (Gould 1966). To study this finally, multivariate static allometric coefficients for the 14 cranial variables were calculated to look at the influence of covariation of shape and form dimensions related to size differentiation (Leamy & Bradley 1982).

In a first step we performed principal component analyses separately for each population sample (Smith & Patton 1988). Because the first principal component (PC1) of our data satisfies interpretation as a general size factor, the position (= score) of an individual on PC1 is a measure of its overall body size, while the "raw" loadings (= elements of the eigenvector)

Table 1: The scored enzymes listed with their tissue source, electrophoretic conditions and encoding loci analyzed.

Enzyme	E. C. Code	Locus Abbreviation	Electric Field	Tissue	Electrophoretic Cond.[1)]	Staining Ref.[2)]
Alcohol dehydrogenase	1.1.1.1	Adh	cathodal	liver	PHOS pH 6.7	B
α-glycerophosphate dehydrogenase	1.1.1.8	Gpdh	anodal	muscle	TC II pH 8	B
Sorbitol dehydrogenase	1.1.1.14	Sordh	anodal	liver	TC II pH 8	D
Lactate dehydrogenase	1.1.1.27	Ldh-1 (subunit A)	anodal	muscle	TC I pH 6.3	A
		Ldh-2 (subunit B)	anodal	muscle	TC I pH 6.3	
Hydroxybutyrate dehydrogenase	1.1.1.30	Hbdh	anodal	liver	TME pH 7.4	B
Malate dehydrogenase	1.1.1.37	Mdh-1	anodal	muscle	TC I pH 6.3	B
		Mdh-2	cathodal	muscle	TC I pH 6.3	
Malic enzyme	1.1.1.40	Me-1, -2	anodal	muscle	TME pH 6.4	B
Isocitrate dehydrogenase	1.1.1.42	Idh-1, -2	anodal	muscle	AC pH 6.1	B
6-Phosphogluconate dehydrogenase	1.1.1.44	6-Pgdh	cathodal	muscle	AC pH 6.1	E
Glucose-6-phosphate dehydrogenase	1.1.1.49	Gd	anodal	muscle	TC I pH 6.3	E
Xanthin dehydrogenase	1.1.1.204	Xdh	anodal	muscle	TC II pH 8	A
Glycollate oxidase	1.1.3.1	Gox	anodal	muscle	TC II pH 8	C
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	Ga3pdh	cathodal	muscle	PHOS pH 6.7	B
Glutamate dehydrogenase (NADP)	1.4.1.4	Glutdhp	anodal	liver	TC II pH 8	D
Diaphorase	1.6.–.–	Dia-2	anodal	liver	TC II pH 8	C
Gluthatione reductase	1.6.4.2	Gsr	cathodal	liver	TC II pH 8	D
Peroxidase	1.11.1.7	Per	anodal	liver	TVB pH 8.0	D
Indophenol oxidase	1.15.1.1	Ipo-1	anodal	liver	TVB pH 8.0	D
		Ipo-2	cathodal	liver	TME pH 7.4	
Succinate dehydrogenase	1.3.99.1	Sucdh	anodal	liver	TVB pH 8.0	D
Nucleoside phosphorylase	2.4.2.1	Np	anodal	liver	TC II pH 8	A
Glutamate-oxaloacetate transaminase	2.6.1.1	Got-1	anodel	muscle	TC II pH 8	E
		Got-2	cathodal	muscle	TC II pH 8	
Glutamate-pyruvate transaminase	2.6.1.2	Gpt	anodal	liver	TVB pH 8.0	C
Tyrosine aminotransferase	2.6.1.5	Tat-1	anodal	liver	TVB pH 8.0	D
		Tat-2	cathodal	liver	AC pH 6.1	
Hexokinase	2.7.1.1	Hk	anodal	muscle	TC II pH 8	E
Pyruvate kinase	2.7.1.40	Pk	anodal	liver	TME pH 7.4	C
Arginine kinase	2.7.3.3	Apk	anodal	muscle	TC II ph 8	D
Creatine kinase	2.7.3.2	Ck	anodal	liver	TME pH 7.4	E
Adenylate kinase	2.7.4.3	Ak	anodal	muscle	TC II pH 8	D
Phosphoglucomutase	2.5.7.1	Pgm-1	anodal	muscle	TC pH 6.3	D
		Pgm-2	cathodal	or liver		
Esterase	3.1.1.–	Est-1, -2, -3	anodal	liver	TVB pH 8.0	A
Acid phosphatase	3.1.3.2	Acph	cathodal	liver	PHOS pH 6.7	D
β-Glucuronidase	3.2.1.31	Glur	anodal	liver	TVB pH 8.0	C
Peptidase	3.4.11.–	Pep-1*, -2, -3**	anodal	muscle	TC II pH 8	A
Guanine deaminase	3.5.4.3	Gda	anodal	liver	TVB pH 8.0	A
Adenosine deaminase	3.5.4.4	Ada	anodal	muscle	TC II pH 8	A
Carbonic anhydrase	4.2.1.1	Ca	cathodal	liver	TVB pH 8.0	D
Enolase	4.2.2.11	Eno	anodal	liver	TME pH 7.4	D
Fumarase	4.2.1.2	Fum	cathodal	liver	TC II pH 8	D
Glyoxalase	4.4.1.5	Glo	cathol	muscle	PHOS pH 6.7	C
Aconitase	4.2.1.3	Acon-1, -2	cathodal	liver	AC pH 6.1	D
Triose phosphate isomerase	5.3.1.1	Tpi	anodal	muscle	TC II pH 8	D
Mannose phosphate isomerase	5.3.1.8	Mpi	anodal	muscle	TC II pH 8	C
Glucose phosphate isomerase	5.3.1.9	Pgi	anodal	muscle	TC II pH 8	E
Serum protein		Prot 3	anodal	liver	TVB pH 8.0	D

1) Buffer systems were as follows: AC pH 6.1 (Amine-Citrate: Clayton & Tretiak 1972): 12 % starch gel, 16 h, 125 V, ~10 mA, ~4 V/cm; — TC I pH 6.3 (Tris-Citrate: Selander et al. 1971): 12 % starch gel, 16 h, 100 V, ~25 mA, ~4 V/cm; — TC II pH 8 (Tris-Citrate: Selander et al. 1971): 12 % starch gel, 110 V, ~13 mA, ~4 V/cm; — TME pH 7.4 (Tris- Maleate-EDTA: Murphy et al. 1990): 12 % starch gel, 16 h, 125 V; ~35 mA, ~4,5 V/cm; — TVB pH 8.0 (Tris-Borate-EDTA (Brewer 1970): Murphy et al. 1990): 12.5 % starch gel, ~125 V, ~8 mA, ~4 V/cm; — PHOS pH 6.7 (Phosphate: Selander et al. 1971): 12 % starch gel, 16 h, 100 V, ~12 mA, ~4 V/cm.

2) Staining references are: A = Aebersold et al. (1987); B = Ayala et al. (1972); C = Harris & Hopkinson (1978); D = Murphy et al. (1990); E = Shaw & Prasad (1970).

* Substrate is leucyl-alanine. ** Substrates are tripeptide Gly-gly-leucine and dipeptide phenylalanyl-l-methionine.

of variables on this component describe the relative contribution of each variable to change in general size, thus are proportional to allometric coefficients of the characters with respect to size (Bookstein et al. 1985). The first principal component of the variance-covariance matrix from log-transformed data should therefore represent some kind of an isometric size vector that can be rescaled to the length of one (Somers 1986) if covariation between the variables approach equality. Where allometry exists, it thus provides a standard measure against which growth trajectories of individual cranial characters can be compared (Smith & Patton 1988).

To "normalize" the first principal component to unity we divided its raw loadings by a value $\Sigma_p k_i^2]^{1/2}$, where k = raw loadings and p = number of cranial variables) such that their squared elements sum up to unity. Then the normalized loadings were divided by $1/\sqrt{p}$ to rescale the loadings to be expected if all dimensions (p = 14) have grown at the same rate (Shea 1985). Resulting positive allometric variables with multivariate adjusted coefficients $>$ 1 are those that are relatively larger in large individuals than in smaller ones; negative allometric variables (coefficients <1) are those with the opposite relationship (Strauss & Bookstein 1982).

Allometric coefficients were used as new variables in a discriminant analysis (employing the MGLH routine of SYSTAT) that treats population samples separately. Canonical variable plots (Fig. 5) give insight into grouping patterns.

Electrophoresis

A total number of 53 animals were caught with snap traps at four localities (no. 1, 2, 9, 10 in Fig. 1). Tissue samples (muscle, liver, heart) were taken in the field and stored in liquid nitrogen until being returned to the ZFMK biochemical laboratory, where they were cut into small pieces and maintained in an ultracold freezer (−85 °C) for long term storage (tissue collection).

Prior to electrophoretic analysis a fivefold volume of 0.1 M Tris/HCl homogenate buffer (pH 7.0) containing 0.002M EDTA and 0.05M NADP was added to the weight of portioned tissue, either pure organ specific probes or mixes from both liver and muscle, which were then homogenized with a motor-driven homogenizer (Polytron dispenser with 12mm shaft, Kinematica, Switzerland) keeping samples cool in an ice-bath. Homogenates were shaken with 0.1 — 0.2ml Toluene and immediately centrifuged for 10 minutes at 13.000g (Biofuge 13, Heraeus-Sepatech, Germany). The clear supernatant (25μl per sample) was transferred onto Micro Test Tissue Culture Plates (COSTAR, Cambridge; Greiner, Germany) and refrozen in a —20 ° freezer until electrophoretically processed.

We employed the procedures of vertical starch gel electrophoresis first described by Smithies (1955) and recently reviewed in Geiger (1990), who also gave details due to technical novelties and apparative equipments. Starch gels are made in concentration of 12 % and 12.5 % (w/v) starch in gel buffer using BIOMOL starch (Hamburg, Germany; Tab. 1). Handling and preparation of gels follows the outlines made by Murphy et al. (1990). Sample application in the vertical apparatus is done by means of an Eppendorf comforpette pipetting amounts of 5—10μl per individual into a preformed slot (20 in total) in the gel, which is then sealed by molten vaseline. Gels were electrophoresed overnight (16 h) at 3−4 V/cm in a 4 °C temperated freezer, the gels additionly connected to an cooling system with cooling plates. Each gel was then sliced into 1.2 mm thick slabs for histochemical overlay-staining adopting the visualization techniques as described by Ayala et al. (1972), Catzeflis et al. (1982), Filipucci et al. (1987), Harris & Hopkinson (1978), Hartl & Höger (1986), Selander et al. (1971) and Shaw & Jain (1970).

44 enzymes and general proteins encoded by 57 presumptive structural gene loci were examined for all populations. Electrophoretic running conditions, separation buffer systems used, enzymes assayed and their tissue sources are listed in Tab. 1; although no progeny testing was routinely done (with the exception of the Kaliningrad area sample KAL) to confirm the mode of inheritance of allozyme variants, resulting zymograms generally conformed with simple patterns of codominant Mendelian inheritance, so that genetic interpretation of banding patterns could easily be done based on principles published by Csaikl (1985), Harris & Hopkinson (1978), Hartl et al. (1988), Richardson et al. (1986) and Selander et al. (1971). Designation of

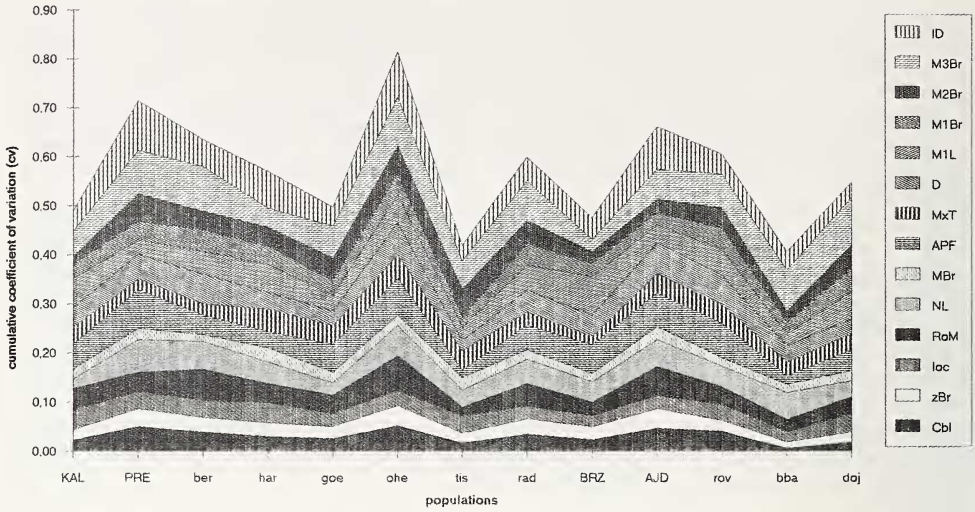

Fig. 3: Banding diagram of coefficients of variations within populations.

encoding loci and allelic variation of the allozymes are as follows: Genes are symbolized by italicizing the enzyme and protein abbreviation of Table 1; numerical suffixes distinguish among multiple zones of cathodal or anodal or both activities on certain zymograms in order of decreasing mobility from the most anodal one considering anodal migration first; electromorphs (interpreted as alleles) were given letters in alphabetical order, arbitrarily starting with the one that migrated the least to the anode (anodal migration) or the least to the cathode (in case of cathodal migrating) under standard electrophoretic conditions as described here (Tab. 6).

General statistical tests

Modified Mantel's (1967) randomization test in a multiple regression and correlation extension was used to test for matrix associations between genetic, geographical and morphological distances among the four populations KAL, AJD, BRZ and PRE, where the distances in one matrix are regressed on the distances in the other matrices (Manly 1991). Significance of correlations between geographic and morphometric distance for all 13 populations in the morphometric study were tested with ordinary Mantel analysis (1967).

Results and discussion

Craniometric analyses

Variation of single variables

Coefficients of variation evidence very low intra-populational differences. The banding diagram (Fig. 3) shows values as low as 0.018 for Cbl in sample Lake Dojran (doj) and a higher value of 0.052 in Osthessen (ohe). As a representative of tooth variables M3Br ranges from 0.052 in Kaliningrad (KAL) to 0.099 in Osthessen. The diagram shows no disruptive geographical trend due to a characterization of certain populations.

Variation in size

Condylobasal length (Cbl) and zygomatic breath (zBr) can be considered the most useful single indicators of overall cranial size among the variables examined. They

are highly correlated with the other skull measurements (less with dentition variables; Tab. 2) and have low within-population coefficients of variation (Fig. 3). For example, condylobasal length means range from 21.46 mm in population Harz, Germany (har) to 24.75 mm in population Lake Dojran, Macedonia (doj), representing a 13.3 % difference among localities.

Although our study is faced with a relatively low degree of variability (Tab. 2), multiple group principal component analysis was effective enough to discriminate between minor morphometrically mensurable differences in cranial size and shape.

In order to analyze size variation among populations in a multivariate treatment, the first two multiple group principal components from the pooled within-group character relationships can be considered as general size factors, since all vector coefficients are positive (tooth variables excluded) and show correlations with the original log-transformed character values (Strauss 1985). The correlation between Cbl, for example and MGPC-1 is 0.936. Communalities of the variables that are the proportions of variance accounted for by the two main factors are given in Tab. 2. Linear skull measurements and tooth variables show almost complete loadings on both components.

To investigate the relationships in the craniometric variables on their own, Table 3 gives the loadings for the three vectors, together with the percentage variation they express (cf. Thorpe & Leamy 1982). The first multiple-group principal component accounts for 36.48 % of the within-group variation across the entire sampled range of *A. agrarius* in Europe, the first three components account for 69.82 % of total variance. MGPC-1 is the largest (36 %) and is equally loaded in magnitude with contributions of the cranial variables ID, D, APF, RoM, NL, Cbl and zBr, but inverse

Table 2: Pearson product-moment correlation coefficients between the mean $\log_{10}$-transformed cranial variables for the 13 population samples of *A. agrarius*, their scores on the first three Principal Component axes extracted by a multiple-group PCA and communality of variables on the first two components (see text for details).

character	PC-1	PC-2	PC-3	communality
log Cbl	0.936	0.695	0.176	0.863
log zBR	0.885	0.674	0.232	0.627
log Ioc	0.554	0.554	0.457	0.054
log RoM	0.854	0.658	0.163	0.621
log NL	0.861	0.643	0.055	0.616
log MBr	0.736	0.708	0.296	0.288
log APF	0.850	0.624	0.128	0.569
log MxT	0.508	0.786	0.505	0.362
log D	0.908	0.615	0.012	0.727
log M1L	0.299	0.563	0.846	0.088
log M1Br	0.349	0.649	0.524	0.228
log M2Br	0.102	0.779	0.393	0.625
log M3Br	0.015	0.825	–0.003	0.904
eigenvalue	0.002	0.001	0.001	
% explained variance	36.48	23.26	10.08	

Table 3: Mean static allometric coefficients for 14 cranial variables for 13 populations of *A. agrarius*.

pop.	CbL	zBr	Ioc	RoM	NL	MBr	APF	MxT	D	M1L	MiBr	M2Br	M3Br	ID
AJD	1.15	0.93	0.01	1.29	1.14	0.32	1.67	0.31	1.39	0.08	0.03	0.03	0.88	1.77
rov	1.30	0.45	0.25	1.05	1.12	0.06	2.17	0.28	1.86	0.42	0.77	0.48	0.03	0.64
BRZ	0.75	0.53	0.51	0.30	1.42	0.41	0.86	0.16	1.64	2.66	0.07	0.06	0.25	0.15
tis	0.03	0.52	0.44	0.22	0.29	0.58	0.33	1.18	0.14	0.25	0.47	2.13	2.59	0.13
ber	1.17	0.48	0.29	1.71	1.47	0.05	0.91	0.28	1.87	0.56	0.35	0.16	1.40	0.61
har	0.90	0.87	1.10	0.99	1.12	0.80	0.01	0.83	0.77	1.15	0.36	0.65	0.85	2.11
PRE	1.05	0.69	0.13	0.74	0.91	0.35	1.07	0.29	1.07	0.16	0.27	0.98	1.87	2.00
goer	0.81	0.59	0.30	0.85	0.27	0.60	1.23	1.05	0.90	0.06	0.33	1.40	2.43	0.59
KAL	0.40	0.49	1.24	1.28	0.16	0.53	1.12	1.04	0.97	2.50	0.74	0.05	0.13	0.15
ohe	0.09	0.21	0.12	0.13	1.41	0.59	0.41	0.93	0.20	0.58	0.81	0.75	2.82	1.00
doj	0.98	0.72	0.16	1.33	0.90	0.28	1.30	0.19	1.16	0.05	0.05	0.88	1.70	1.76
rad	0.08	0.29	0.13	0.46	0.07	0.06	0.36	0.82	0.09	1.46	0.74	1.24	2.91	0.40
bba	1.07	0.98	0.10	1.11	1.38	0.41	1.34	0.63	1.39	0.24	0.79	0.59	1.40	1.21

Table 4: Values of intrapopulational genetic variation.

				mean heterozygosity H	
population	mean sample size per locus	mean no. of alleles per locus	proportion of loci polymorphic ($P_{5\%}$)*	direct-count (H_O)	under Hardy-Weinberg equilibrium (H_e)**
Prenzlau	14.5±0.5	1.2±0.1	0.211	0.095±0.024	0.092±0.024
Brezice	13.9±0.4	1.2±0.1	0.228	0.092±0.022	0.092±0.025
Kaliningrad	7.4±0.2	1.2±0.0	0.158	0.064±0.023	0.066±0.021
Ajdovscina	12.9±0.4	1.2±0.1	0.175	0.057±0.017	0.079±0.022

* A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.95
** unbiased estimate (see Nei, 1987)

correlation by dentition features, emphasizing independence of overall size. The second component is dominated by tooth variables (M3Br, M2Br) with less emphasis of size contributions from the remaining skull variables. The third component is displaying portions of shape variation, expressed through varying and inverse correlations between variables rendering very low explained variance. Although all variables in total contribute most to linear size relationships, there are two principal sets of variables, dentition and linear skull measurements, that vary non-concordant according to size and shape dimensions. Dentition is mainly independent of individual size in rodents, as expected from the developmental stability of ontogenetic growth of the molar dentition, and shows no aptitude to be influenced by environmental factors.

Geographic variation of size

The scores from the first two principal components for the individuals of each population can be used as a multivariate measure of cranial size (Tab. 3). Striped field mice have largest skulls in populations Lake Dojran (doj) and Rovinj (rov), and smallest in population Harz (har). Mean scores per population increase along the MGPC-1 axis from 1.85 in the smallest *agrarius* populations (har) to ca. 2.15 in the *kahmanni* population (doj) and the *istrianus* population (rov) (Tab. 6). We found a linear population overlap along a mainly size varying array in direction of the MGPC-1 axis, although the sequence is also mostly influenced by loadings from the tooth variables that direct separation along the second MGPC axis (Fig. 4). Means of M2Br are smallest in population Osthessen (ohe: 1.05 mm) and largest in Rovinj (rov: 1.19 mm), for M3Br the smallest average was again found in Osthessen with 0.69 mm, and the largest in population Banja Bansko (bba) with 0.83 mm. There is a slightly small gap between the *agrarius* pool and both *kahmanni* and *istrianus* samples. The same is true for the individual scores grouped according to subspecies (Fig. 4).

In the bivariate plot of the first canonical variable against CV-2 in the "size-out" analysis, all differences between the populations are blurred as compared to the size-related discrimination described above (Fig. 5). Exactly the same results are gained after adjusting the data with Burnaby's discriminant approach, i. e. when most variation through size differences between populations were removed from the first principal component. Remaining variability left no more clear-cut structure to discriminate among groups (not shown here). Eliminating size from the data by means of both methods yielded clouds of component scores leaving the populations indistinguishable from one another in character space.

Discriminant analysis

A discriminant analysis was performed with populations grouped according to the currently recognized subspecies. Canonical variable functions found are useful to clearly separate between *agrarius*, *istrianus* and *kahmanni*. The *agrarius* group is very well separated from the *istrianus* and *kahmanni* samples, showing small overlap (Fig. 6). As many as 153 of the 158 animals were correctly assigned to the reference subspecies (96.2 %). Problems only occurred with the identification of *istrianus* and *kahmanni*.

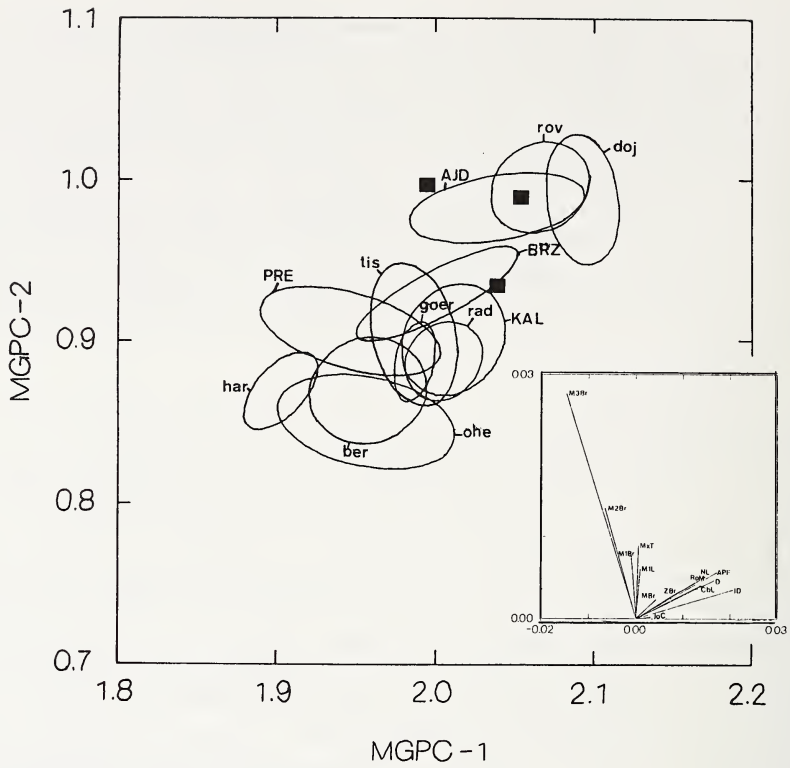

Fig. 4: Bivariate plot of the 95 % confidence ellipses for the sample means of the first two principal component factor scores of 13 populations of *A. agrarius* derived from a multiple-group PCA. The proportion of total variation explained by each component is indicated. The inset illustrates character vectors, based on their respective correlations with these axes.

When the samples were grouped only after their geographic origin, the separation of the three subspecies turned out less clearly (Fig. 7); 12 (19 %) animals were ill-classified, but 48 % could be classified correctly out of 13 populations, showing a high degree of variability. The same result is shown by the Neighbour-Joining tree based on the Mahalanobis distances of individual canonical variable scores from group centroids. Only a separation of the *istrianus/kahmanni* group on the one hand and *agrarius* on the other hand can be ensured. The branching pattern within the *agrarius* group displays no significant evidence.

In general, discriminant analysis is a very useful tool to find or contrast differences between groups. However, a pre-allocation to a certain group should always be based on hard evidence. It is not advisable to introduce information into the calculations that should be confirmed by the following analysis. One should avoid an assignment of individuals to subspecies if the purpose of the analysis is to look for subspecific differentiation. Results of the discriminant analysis therefore should not be taken as affirmative because they are biased by a priori information. In this case multiple group principal component analysis revealed a convergent size shaping of W Slove-

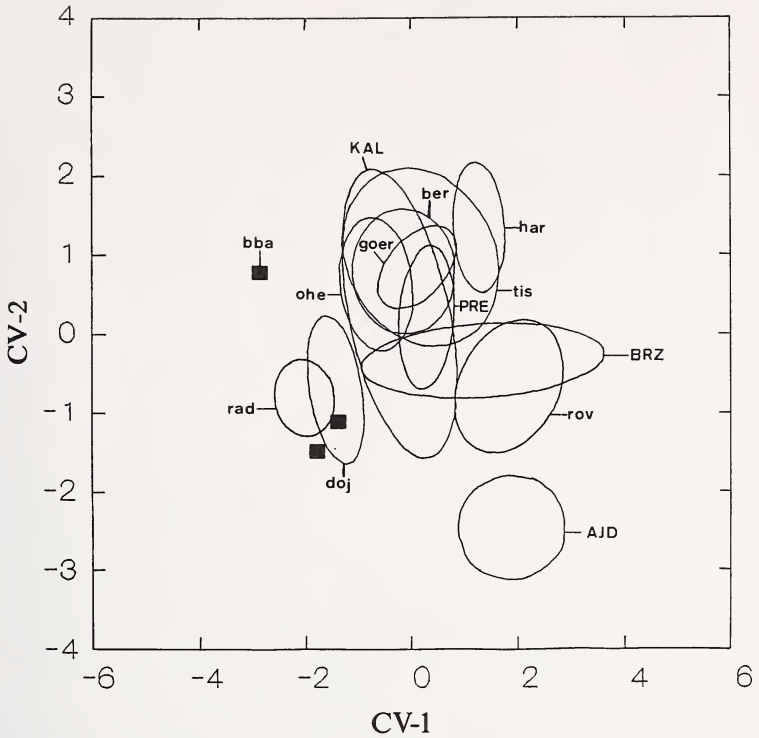

Fig. 5: Bivariate plot of 95 % confidence ellipses for canonical variate scores on the first 2 axes derived from a canonical analysis of the cranial "size-out" variables MGPC-3 through —14 for the 13 populations of *Apodemus agrarius*.

nian and Macedonian populations, not recognized by discriminant analysis. The phenomenon of phenotypically similar populations in disparate geographic areas is well known (Mayr 1975).

Static allometric coefficients

As MGPC-1 accounts primarily for variation in size, its loading reflecting average size-related changes among the samples, mean static allometric coefficients likewise indicate the manner in which different measurements change in relation to overall body size. The allometry values for each of the 14 cranial variables are given in Tab. 3. We used these allometric coefficients to explore components of genetic programs that may underly morphological trait expression and may rule individual growth trajectories within populations or population groups (= subspecies). To address these questions, the static allometric coefficients were used as variables in a discriminant analysis with a priori allocation of individuals to the three presumed subspecies. As a result, each population sample could be distinguished by a unique set of character allometries and their allocation to certain subspecies was with absolute a posteriori certainty. However, plotting the first two canonical variables against each other, we found three groupings (Fig. 8). Midway lie most *agrarius* populations, flanked by the

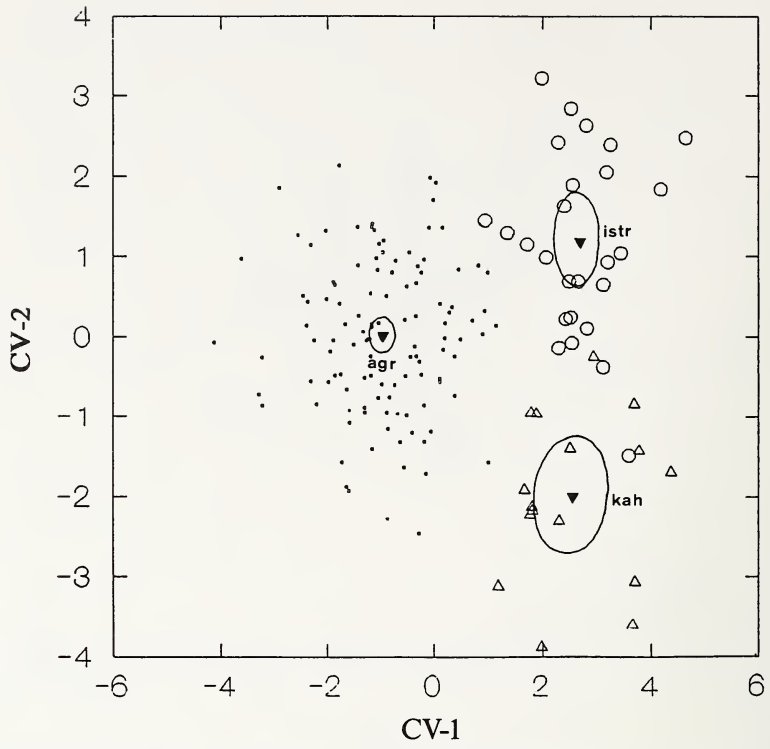

Fig. 6: 95 % confidence ellipses surrounding canonical variate scores of the first two discriminant functions for the three subspecies groups.

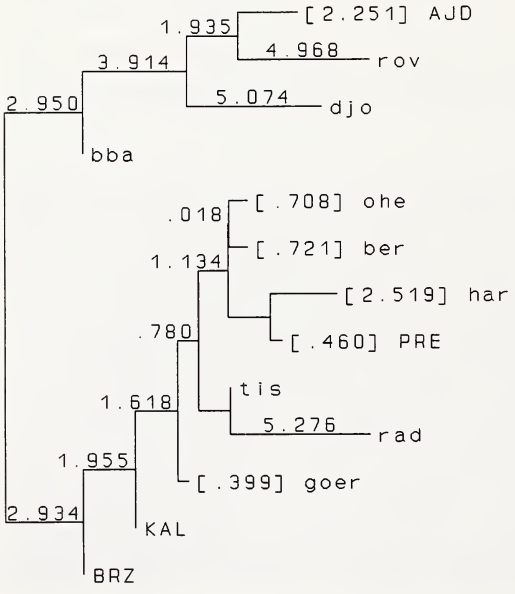

Fig. 7: Neighbour-Joining tree based on Mahalanobis D^2 of the morphological distances among the 13 populations of *A. agrarius*.

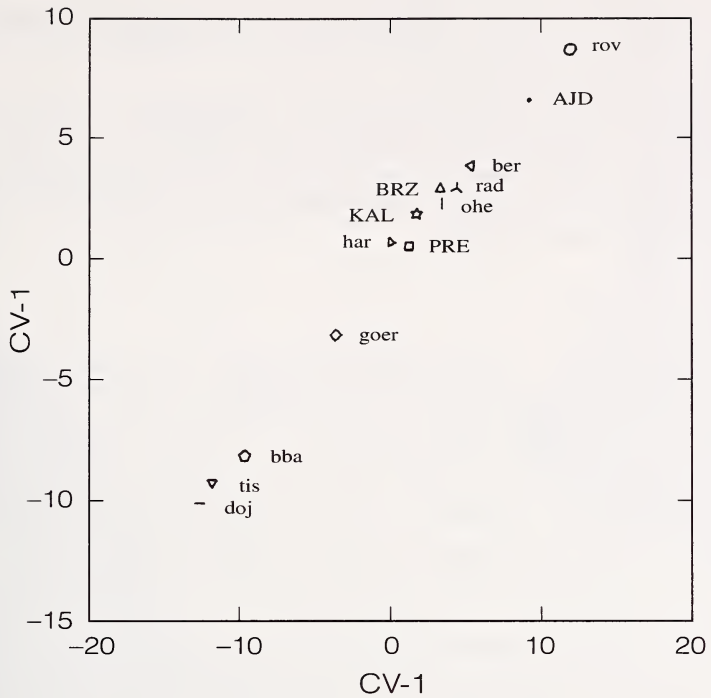

Fig. 8: Plot of the 13 populations against their values for two canonical discriminant functions derived from the populations' mean static allometric coefficients (see text for details).

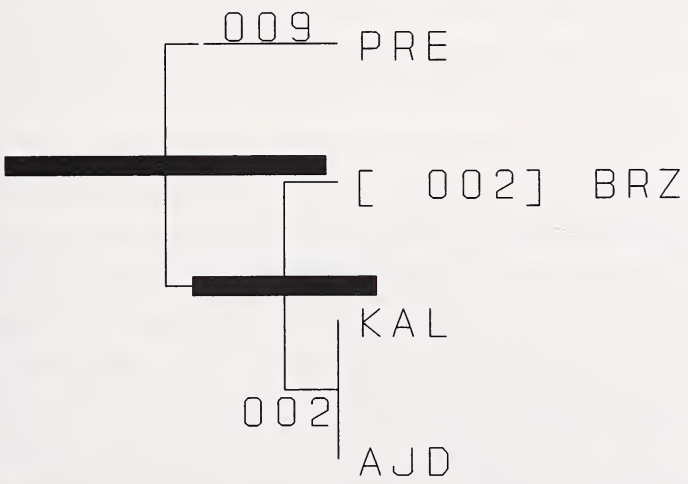

Fig. 9: UPGMA-phenogram based on Nei's unbiased genetic distances between 4 populations.

istrianus populations which rise to higher values, and the *kahmanni* populations with decreasing values on both axes. The latter group also contains the *agrarius* population Tiszacsege (tis) from Hungary.

We again found highly informative allometric relationships to characterize individual populations. Reasons for this may be that *A. agrarius* can quickly adapt its growth to changing environmental conditions. Skull dimensions appear to be very easily transformed when different food ressources are exploited, for instance in urban green areas (Sikorski 1982).

Electrophoretic analysis

Genetic distances (Nei's unbiased standard measure D), sample size per locus, percentage polymorphic loci, and direct-count and expected mean heterozygosity under a Hardy-Weinberg equilibrium are listed in Table 4. Electrophoresis indicates a low level of variation both within and among populations. Of 57 loci analyzed, twenty-seven were fixed for the same allele in all populations screened for protein variation. The remaining variable loci were each polymorphic for two alleles recombined in different genotype frequencies (Tab 6). A third allele (c) of the enzyme Gpt (rf = 38 mm) was detected in all populations but Ajdovscina. On average, we found 1.2 alleles per population.

The number of loci expressing variation within populations ranged from 15.8 % (KAL) to 22.8 % (BRZ), using a 5 % frequency cutoff level. Direct-count heterozygosity per population ranged from 0.057 ± 0.017 in population Ajdovscina to 0.095 ± 0.027 in population Prenzlau. All populations display strikingly low values of genetic distances (D ranges from 0.009 to 0.040).

Values of genetic variation are within the range reported in previous work on *A. agrarius* (Filipucci 1992; Britton-Davidian et al. 1991). The latter authors, who studied *kahmanni* populations from Greece and Bulgaria, especially considered genetic distances as falling within the values generally recorded for subspecific genetic differentiation, whereas Filipucci (1991) contrasted this opinion by stating that "a relatively low value of genetic distance (D = 0.027) was observed among the populations of *A. agrarius*, which are attributed to different subspecies: *A. a. istrianus* and *A. a. agrarius* ...".

We conclude from our findings that genetic variability values clearly demonstrate an amount of genetic differentiation to be found in local populations of a species with a high level of gene flow among conspecific populations. Clusters do not indicate any significant branches among the populations (see error bars in Fig. 9), as must be expected when certain subspecies are involved. A very limited degree of differentiation over its range can often be found in species with distribution patterns of a typical Euro-Siberian faunal element (de Lattin 1967), as *A. agrarius* can be described. Zhao & Lu (1986), for example, reported on a similar mobility variation in serum proteins among Chinese populations of *A. agrarius*. Direct count heterozygosity of population Ajdovscina, however, provides evidence of a genetic discontinuity concerning a highly significantly lowered mean level of gene diversity (one-tailed $t_{[0.01;\,115]} = 4.89$), as compared to the E Slovenian population Brezice, indicating an isolated gene pool.

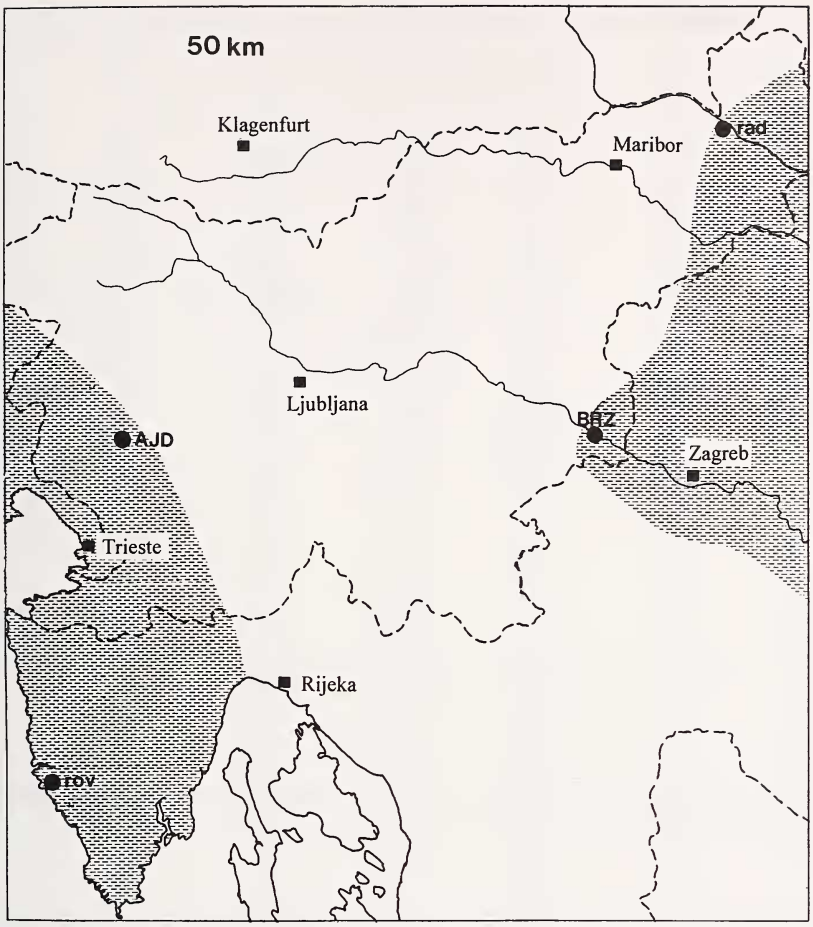

Fig. 10: The samples AJD, rov, BRZ and rad and the local distribution patterns of *A. agrarius* in the northern Balkans (shaded) (after Krystufek 1991 and Petrov 1992).

Mantel test on distance matrices

The relationship between populations of *A. agrarius* in Europe based on morphological, genetical and geographical distances was studied in a subset of four populations. The Mantel test was performed to test for statistical association between three distance matrices. Morphological distance is represented by Mahalanobis D^2 between the 4 populations previously derived from the discriminant analysis of the log-transformed cranial variables. Nei's unbiased genetic standard distance reflects genetic differences, and geographic distances were measured as straight air line distances between localities.

We did not find any high Pearson correlation coefficients to indicate significant intercorrelated associations between matrices. The reason may be the restricted data

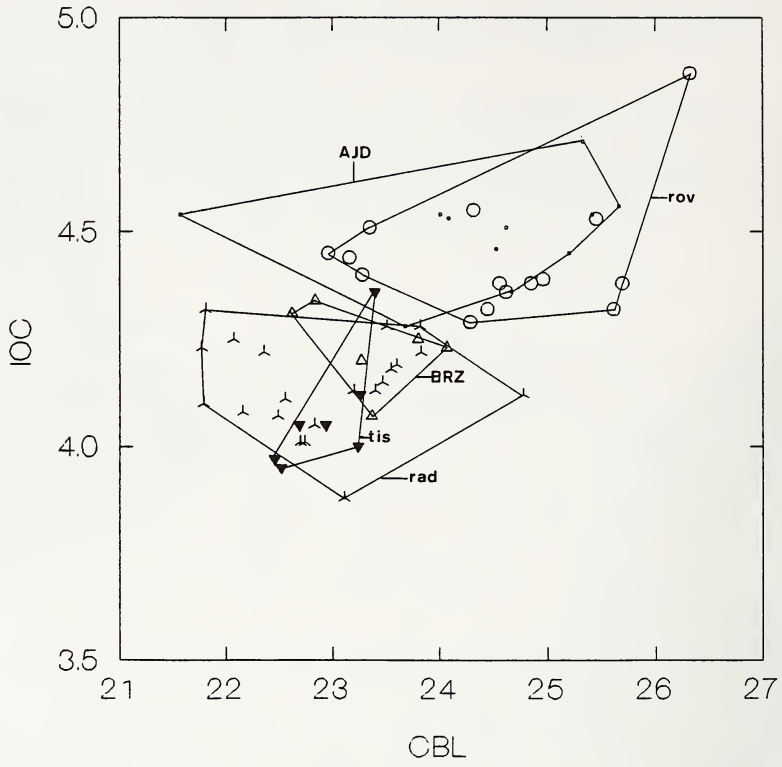

Fig. 11: Scatter diagram of CbL against IoC for W (AJD, rov) and E Slovenian (BRZ, rad) populations of *A. agrarius*.

set of only four populations, including the Slovenian populations BRZ and AJD that show a relatively higher proportion of morphological difference in relation to their actual geographic distances (about 120 km), as compared to the other populations studied (Fig. 10). When CbL is plotted against IoC, W and E Slovenian populations are clearly different (Fig. 11); their morphological divergence is as great as that between German and Macedonian populations (Fig. 7).

Ordinary Mantel test on significance probability of matrix association between morphological and genetic distances between all populations gave over 95 % correlation ($p = 0.0265$), testifying that the the morphological differentiation increases with distance between populations.

Conclusions: body size variation, genetics and systematics

In phenetic analyses of geographic variation, one looks for geographic character patterns which components reflect simple plastic responses to local environmental conditions to clearly distinguish them from fundamental adaptive genetic changes which fit the requirements of the subspecies concept. In this context a first step is

Table 5: Means, standard deviations, coefficients of variation and range of the craniometric measurements within 13 populations of *A. agrarius*.

var.	pop.	mean	sd	cv	min	max
Cbl	KAL	22.90	0.53	0.02	22.25	23.55
	PRE	22.07	1.10	0.05	20.03	23.57
	ber	21.96	0.86	0.04	20.23	23.11
	har	21.46	0.65	0.03	20.13	22.32
	goer	22.65	0.58	0.03	21.53	23.58
	ohe	21.84	1.15	0.05	20.15	23.94
	tis	22.93	0.38	0.02	22.46	23.40
	rad	22.93	0.03	0.04	21.77	24.78
	PRZ	23.33.	0.55	0.02	22.62	24.07
	AJD	24.43	1.14	0.05	21.57	25.41
	rov	24.52	1.01	0.04	22.96	26.32
	bba	23.52	0.11	0.01	23.43	23.64
	doj	24.75	0.46	0.02	23.92	25.29
zBr	KAL	12.30	0.24	0.02	11.97	12.41
	PRE	11.74	0.43	0.04	10.96	12.52
	ber	11.69	0.35	0.03	11.04	12.28
	har	11.38	0.32	0.03	10.86	11.88
	goer	12.11	0.30	0.02	11.66	12.63
	ohe	11.77	0.48	0.04	10.95	12.56
	tis	11.91	0.24	0.02	11.56	12.35
	rad	12.23	0.03	0.03	11.75	13.16
	PRZ	12.33	0.32	0.03	11.78	12.75
	AJD	12.94	0.52	0.04	11.59	13.44
	rov	12.71	0.27	0.02	12.20	13.13
	bba	12.58	0.18	0.01	12.38	12.72
	doj	13.10	0.27	0.02	12.72	13.48
Ioc	KAL	4.13	0.16	0.04	3.87	4.36
	PRE	4.13	0.14	0.03	3.88	4.30
	ber	4.16	0.14	0.03	3.95	4.44
	har	4.04	0.17	0.04	3.66	4.27
	goer	4.09	0.11	0.03	3.93	4.32
	ohe	4.10	0.12	0.03	3.87	4.33
	tis	4.07	0.14	0.03	3.95	4.36
	rad	4.14	0.03	0.03	3.88	4.32
	PRZ	4.23	0.10	0.02	4.07	4.34
	AJD	4.50	0.11	0.03	4.28	4.71
	rov	4.44	0.14	0.03	4.29	4.87
	bba	4.30	0.09	0.02	4.21	4.39
	doj	4.34	0.16	0.04	4.13	4.64
RoM	KAL	4.85	0.22	0.05	4.55	5.23
	PRE	4.86	0.19	0.04	4.42	5.14
	ber	4,76	0.31	0.06	4.29	5.32
	har	4.51	0.18	0.04	4.15	4.83
	goer	4.95	0.19	0.04	4.65	5.38
	ohe	4.74	0.34	0.07	4.17	5.25
	tis	5.05	0.10	0.02	4.93	5.16
	rad	4.95	0.05	0.05	4.63	5.56
	PRZ	5.04	0.14	0.03	4.80	5.19
	AJD	5.45	0.33	0.06	5.02	5.91
	rov	5.29	0.20	0.04	5.02	5.65
	bba	5.05	0.13	0.03	4.97	5.20

Table 5 (continued)

var.	pop.	mean	sd	cv	min	max
	doj	5.40	0.19	0.04	4.55	5.23
NL	KAL	9.35	0.18	0.02	9.01	9.54
	PRE	8.94	0.59	0.07	8.02	9.77
	ber	8.95	0.50	0.06	7.79	9.47
	har	8.64	0.38	0.04	8.01	9.19
	goer	9.22	0.23	0.03	8.73	9.79
	ohe	8.96	0.55	0.06	7.88	10.12
	tis	9.55	0.32	0.03	9.12	10.09
	rad	9.17	0.05	0.05	8.30	10.32
	PRZ	9.45	0.39	0.04	9.01	10.00
	AJD	9.63	0.53	0.06	8.58	10.26
	rov	9.96	0.41	0.04	9.24	10.71
	bba	10.17	0.55	0.05	9.60	10.70
	doj	10.40	0.35	0.03	9.71	11.19
MBr	KAL	9.28	0.17	0.02	8.97	9.49
	PRE	9.14	0.21	0.02	8.81	9.47
	ber	9.01	0.13	0.01	8.75	9.23
	har	9.05	0.27	0.03	8.67	9.45
	goer	9.17	0.19	0.02	8.66	9.48
	ohe	9.00	0.19	0.02	8.78	9.43
	tis	9.18	0.24	0.03	8.82	9.40
	rad	9.28	0.02	0.02	8.98	9.60
	PRZ	9.39	0.16	0.02	9.08	9.56
	AJD	9.67	0.25	0.03	9.21	10.04
	rov	9.67	0.16	0.02	9.27	9.81
	bba	9.72	0.17	0.02	9.58	9.90
	doj	9.75	0.20	0.02	9.48	10.24
M3Br	KAL	0.72	0.04	0.05	0.65	0.76
	PRE	0.77	0.07	0.09	0.60	0.87
	ber	0.72	0.06	0.09	0.54	0.79
	har	0.73	0.03	0.04	0.68	0.79
	goer	0.72	0.05	0.07	0.63	0.79
	ohe	0.69	0.07	0.10	0.52	0.79
	tis	0.75	0.04	0.06	0.71	0.84
	rad	0.71	0.08	0.08	0.54	0.82
	PRZ	0.76	0.02	0.03	0.73	0.79
	AJD	0.80	0.05	0.06	0.73	0.90
	rov	0.80	0.06	0.07	0.71	0.87
	bba	0.83	0.07	0.08	0.76	0.90
	doj	0.79	0.08	0.10	0.68	0.90
ID	KAL	1.27	0.05	0.04	1.20	1.33
	PRE	1.16	0.12	0.10	1.01	1.36
	ber	1.24	0.07	0.06	1.09	1.33
	har	1.16	0.09	0.08	1.03	1.31
	goer	1.26	0.05	0.04	1.20	1.36
	ohe	1.23	0.11	0.09	1.01	1.39
	tis	1.21	0.04	0.03	1.17	1.28
	rad	1.24	0.05	0.05	1.09	1.33
	PRZ	1.23	0.05	0.04	1.17	1.31
	AJD	1.30	0.11	0.09	1.14	1.50
	rov	1.42	0.06	0.04	1.31	1.52

Table 5 (continued)

var.	pop.	mean	sd	cv	min	max
	bba	1.36	0.05	0.04	1.31	1.41
	doj	1.47	0.05	0.03	1.41	1.58
M1L	KAL	2.17	0.13	0.06	1.93	2.29
	PRE	2.14	0.06	0.03	2.07	2.29
	ber	2.01	0.09	0.05	1.80	2.15
	har	2.07	0.12	0.06	1.93	2.31
	goer	2.09	0.07	0.03	1.96	2.20
	ohe	2.02	0.12	0.06	1.82	2.26
	tis	1.97	0.06	0.03	1.85	2.01
	rad	2.01	0.05	0.05	1.85	2.26
	PRZ	2.18	0.17	0.08	1.96	2.45
	AJD	2.23	0.08	0.04	2.07	2.37
	rov	2.29	0.12	0.05	2.10	2.50
	bba	2.04	0.05	0.02	1.99	2.07
	doj	2.14	0.12	0.06	1.96	2.37
M1Br	KAL	1.18	0.04	0.03	1.17	1.22
	PRE	1.17	0.04	0.04	1.09	1.25
	ber	1.16	0.05	0.04	1.09	1.22
	har	1.18	0.04	0.04	1.06	1.22
	goer	1.17	0.04	0.03	1.10	1.22
	ohe	1.18	0.05	0.04	1.12	1.31
	tis	1.20	0.03	0.02	1.17	1.22
	rad	1.21	0.04	0.04	1.09	1.31
	PRZ	1.19	0.03	0.03	1.14	1.22
	AJD	1.26	0.03	0.03	1.22	1.31
	rov	1.28	0.05	0.04	1.22	1.39
	bba	1.20	0.03	0.02	1.17	1.22
	doj	1,24	0.06	0.05	1.14	1.36
M2Br	KAL	1.08	0.02	0.02	1.06	1.09
	PRE	1.10	0.06	0.06	0.93	1.14
	ber	1.07	0.04	0.04	1.01	1.14
	har	1.11	0.04	0.04	1.03	1.20
	goer	1.08	0.05	0.04	1.03	1.17
	ohe	1.05	0.06	0.06	0.87	1.12
	rad	1.05	0.05	0.05	0.95	1.14
	PRZ	1.13	0.03	0.02	1.09	1.17
	AJD	1.16	0.03	0.03	1.12	1.22
	rov	1.19	0.05	0.04	1.14	1.33
	bba	1.12	0.03	0.02	1.09	1.14
	doj	1.13	0.05	0.05	1.03	1.20
APF	KAL	4.86	0.25	0.05	4.58	5.30
	PRE	4.58	0.36	0.08	3.95	5.12
	ber	4.45	0.18	0.04	4.18	4.70
	har	4.21	0.14	0.03	3.97	4.39
	goer	4.53	0.26	0.06	4.05	5.03
	ohe	4.33	0.33	0.08	3.87	5.09
	tis	4.64	0.07	0.02	4.56	4.79
	rad	4.77	0.05	0.05	4.40	5.33
	PRZ	4.69	0.28	0.06	4.28	5.01
	AJD	4.90	0.34	0.07	4.30	5.29
	rov	5.12	0.36	0.07	4.66	5.74

Table 5 (continued)

var.	pop.	mean	sd	cv	min	max
	bba	4.80	0.09	0.02	4.72	4.89
	doj	5.12	0.21	0.04	4.78	5.48
MxT	KAL	3.67	0.13	0.03	3.50	3.83
	PRE	3.71	0.78	0.02	3.58	3.86
	ber	3.67	0.08	0.02	3.54	3.80
	har	3.65	0.17	0.05	3.32	3.93
	goer	3.68	0.14	0.04	3.42	3.97
	ohe	3.59	0.17	0.05	3.27	3.84
	tis	3.63	0.14	0.04	3.44	3.85
	rad	3.80	0.03	0.03	3.62	4.01
	PRZ	3.70	0.06	0.02	3.63	3.79
	AJD	3.95	0.15	0.04	3.80	4.23
	rov	3.94	0.15	0.04	3.75	4.22
	bba	3.94	0.11	0.03	3.84	4.05
	doj	4.05	0.14	0.03	3.82	4.27
D	KAL	7.11	0.29	0.04	6.82	7.64
	PRE	6.73	0.34	0.05	6.09	7.32
	ber	7.53	0.40	0.06	5.79	6.99
	har	6.17	0.21	0.03	5.78	6.50
	goer	7.78	0.20	0.03	6.48	7.10
	ohe	6.56	0.43	0.07	5.93	7.29
	tis	6.86	0.14	0.02	6.75	7.15
	rad	7.08	0.04	0.04	6.69	7.73
	PRZ	7.17	0.31	0.04	6.81	7.62
	AJD	7.26	0.45	0.06	6.11	7.82
	rov	7.41	0.44	0.06	6.60	8.20
	bba	7.17	0.25	0.03	7.01	7.45
	doj	7.56	0.23	0.03	7.16	7.80

KAL: Zehlau, Kaliningrad area, GUS (n = 7); PRE: Prenzlau, Brandenburg, Germany (n = 12); ber: Berlin, Germany (n = 13); har: Harz, Lower Saxony, Germany (n = 15); goer: Görlitz, Saxony, Germany (n = 18); ohe: Osthessen, Germany (n = 16); tis: Tiszacsege, Hortobagy, Hungary (n = 7); rad: Radenci, Mura rijeka, Slovenia (n = 21); BRZ: Brezice, Slovenia (n = 6); AJD: Ajdovscina, Slovenia (n = 11); rov: Rovinj, Croatia (n = 15); bba: Banja Bansko, Macedonia (n = 3); doj: Lake Dojran, Macedonia (n = 13).

Table 6: List of loci, electrophoretic mobility (rf-values [mm]) and interpreted genotypes detected in the 4 populations of *A. agrarius*.

locus	genotypes	mobility [rf]	Prenzlau (n = 16)	Brezice (n = 15)	Kaliningrad (n = 8)	Ajdovscina (n = 14)
			observed numbers			
Acon1-1	AA	—2	8	8	0	2
	AB		5	4	4	2
	BB	—8	3	3	4	9
Prot 3	AA	57	4	13	7	12
	AB		9	2		1
	BB	61	0	0		0
Dia-2	AA	40	2	3	2	4
	AB		8	4	3	5
	BB	46	6	7	3	4
Est-1	AA	17	3	6	1	7
	AB		9	7	7	6
	BB	24	4	2	0	1
Est-2	AA	45	4	3	8	10
	AB		5	6		1
	BB	54	0	3		0
Est-3	AA	69	14	12	8	11
	AB		1	2		1
	BB	74	0	1		0
Glo	AA	—14	7		1	2
	AB		3		3	1
	BB	—18	5	6	2	8
Gpt	AA	17	0	3	1	4
	AB		4	2	3	6
	AC		1	0	0	4
	BB	27	6	2	4	0
	BB	27	6	2	4	0
	BC		5	7	0	0
	CC	38	0	1	0	0
Me-2	AA	20	0	13	7	11
	AB		4	2	1	2
	BB	27	11	0	0	0
Mdh-1	AA	48	16	15	4	14
	AB				4	
	BB	55			0	
Mpi	AA	26	3	11	8	
	AB		13	4		
	BB	33	0	0		
Pep-3	AA	58		3	2	4
	AB			2	0	4
	BB	62		7	4	1
Pgm-1	AA	4	11	8	5	8
	AB		5	7	3	5
	BB	10	0	0	0	0
Tat-1	AA	51	2	5	3	4
	AB		1	2		3
	BB	59	1	3		2
Xdh	AA	16	5	0		2
	AB		2	2		3
	BB	22	0	1	4	1
monomorphic loci						
Acon-2	AA	—14	15	11	6	11
Acph	AA	—19	16	15	8	14
Ada	AA	85	16	15	8	14
Adh	AA	—32	16	15	8	14
Ak	AA	6	16	15	8	14
Apk	AA	7	16	15	8	14
Ca	AA	—15	16	15	8	14
Ck	AA	18	16	15	8	14
Eno	AA	4	16	15	8	14
Fum	AA	—11	16	15	8	14
Ga3pdh	AA	—8	16	15	8	14
Gd	AA	23	15	15	8	14

Table 6 (continued).

locus	genotypes	mobility [rf]	Prenzlau (n = 16)	Brezice (n = 15)	Kaliningrad (n = 8)	Ajdovscina (n = 14)
			observed numbers			
Gda	AA	72	16	15	8	14
Glur	AA	19	8	5	4	3
Glutdhp	AA	43	16	15	8	14
Got-1	AA	27	16	15	8	14
Got-2	AA	—20	16	15	8	14
Gox	AA	40	12	10	5	8
Gpdh	AA	32	16	15	8	14
Gsr	AA	—4	16	15	8	14
Hbdh	AA	25	8	8	6	12
Hk	AA	55	16	15	8	14
Idh-1	AA	25	16	15	8	14
Idh-2	AA	56	16	15	8	14
Ipo-1	AA	33	16	15	8	14
Ipo-2	AA	—26	16	15	8	14
Ldh-1	AA	18	16	15	8	14
Ldh-2	AA	73	16	15	8	14
Mdh-2	AA	—25	16	15	8	14
Me-1	AA	10	16	15	8	14
Np	AA	53	16	15	8	14
Pep-1	AA	24	16	15	8	14
Pep-2	AA	43	16	13	8	14
Per	AA	35	16	15	8	14
6-Pgdh	AA	—11	16	15	8	14
Pgi	AA	19	16	15	8	14
Pgm-2	AA	—8	16	15	8	14
Pk	AA	—7	16	15	8	14
SorDh	AA	4	16	15	8	14
Sucdh	AA	35	16	10	7	14
Tat-2	AA	—35	11	14	6	12
Tpi	AA	36	16	15	8	14

to part morphometrical variation into size and shape components. Size is more likely to be affected by fluctuations of the external environment, whereas differences in body proportions generally provide more reliable indications of internal, genetically controlled, shape building processes (Boone et al. 1993).

To establish subspecies as infraspecific evolutionary units one ought to find genetic divergence. From the genetical point of view colonization events in historical times can be invoked to explain the low degree of genetic differentiation. *A. agrarius* is supposed to have expanded its range into western Europe from eastern central settlements since about 7000 A. D. (Böhme 1978). Time to diverge in the newly occupated areas has therefore been too short to generate genetic variation that can be detected with genetic distance measures. Gene flow across the populations has probably never been interrupted so long. In this study we found significantly reduced heterozygosity within the W Slovenian population (AJD) as an indication of recent isolation and the potential for evolutionary independence.

Looking at heritable portions within morphological traits some features of the dentition (M2Br, M3Br) seem to be relatively stable against modificatory adaptability of skull dimensions. Molars have equal size in *kahmanni* and *istrianus* populations, and these population groups which have no geographical contact are possibly

expressing similar genetical characteristics that must have been developed independently in both gene pools.

The most obvious fact from our study is a clinal size variation that increases from north to south with W Slovenian and Macedonian populations showing about the same size. These populations have been named as subspecies *istrianus* (Krystufek 1985) and *kahmanni* (Malec & Storch 1963). We actually cannot follow the argumentation of Kahmann & Einlechner (1992), based solely on size criteria, to synonymize the subspecies *istrianus* with *kahmanni*, because there exists a distributional gap in Istria (Fig. 10) documented by Krystufek (1985, 1991), but a continuous distribution from E Slovenia to Macedonia (Petrov 1992). From our point of view, *kahmanni* simply could be the final chain-element of a clinal size variation that suffers from non-genetical environmental impact (see Fig. 8: similar allometric growth of Hungarian and Macedonian populations). Considering *istrianus*, there is enough geographical, morphological and genetic divergence to warrant subspecific nomination of the NE Italian and W Slovenian populations as *A. a. istrianus*.

To test the hypothesis that *kahmanni* is part of the *agrarius* gene pool and that *istrianus* is an isolated population group with subspecific status, it may be useful to investigate craniometrically and electrophoretically samples originating from the area between E Slovenia and Macedonia.

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Zusammenfassung

An Stichproben von 13 europäischen Populationen der Brandmaus aus Deutschland, GUS, Slovenien, Kroatien, Mazedonien und Ungarn wurden 14 Schädelmaße für eine multivariate morphometrische Analyse (Mehrfach-Gruppen-Hauptkomponentenanalyse, lineare Diskriminanzanalyse, statische Allometriekoeffizienten) genutzt, um morphologische Differenzierungen aufzuzeigen, auf deren Grundlage die bisherige infraspezifische Gliederung der Art diskutiert wird. Außerdem wurden 4 Populationen enzymelektrophoretisch untersucht (Berechnung genetischer Abstände auf der Basis von 57 Enzymloci), um ein genetisches Korrelat zur morphologischen Variabilität zu bekommen, mit dem das Ausmaß des Genflusses zwischen den Populationen abzuschätzen ist. Anhand dieser enzymphänotypisch bzw. über Proportionalitätsänderungen der kraniometrischen Variablen aufzeigbaren Unterschiede wird die Nützlichkeit subspezifischer Abgrenzungen unter dem Aspekt evolutiver Eigenentwicklungen infolge geographischer Isolation bzw. unterschiedlicher Besiedlungsfolgen untersucht. *A. agrarius* weist eine nur geringe genetische Variabilität auf, die kaum Rückschlüsse auf subspezifische Differenzierungen zuläßt. Die morphologische Analyse zeigte vor allem größenabhängige Differenzierungen mit vermutlich modifikatorisch bedingten Ausprägungen, welche als Grundlage für die bisherige subspezifische Gliederung dienten. Alle festgestellten Einzelbefunde deuten darauf hin, daß *A. agrarius kahmanni* aus Mazedonien Kontakt zu Populationen der Nominatform hat und wahrscheinlich lediglich das Endglied einer klinalen Größenzunahme in nord-südlicher Richtung darstellt. Dagegen ist *A. agrarius istrianus* aus Slovenien

von dem restlichen Verbreitungsgebiet der Art getrennt, was in einem hochsignifikant herabgesetzten Heterozygotiegrad und einer deutlich morphologischen Differenzierung, konvergent zu *A. a. kahmanni*, zum Ausdruck kommt.

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